Sex-related spatial segregation along environmental gradients in the dioecious conifer, Taxus baccata

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Abstract

Sex-related differences in dioecious woody plants commonly result in spatial segregation of the sexes and a male-biased sex ratio, leading to strongly structured populations. We report results from more than 1000 precisely georeferenced individuals of a threatened European dioecious tree species, *Taxus baccata* in central Italy. We hypothesized differences between males and females in both spatial distribution and growth pattern. We used point pattern analysis (PPA) to evaluate the spatial distribution of trees as influenced by dioecy and tree size, and dendrochronological methods to study growth pattern differences between males and females. We found a dominance of female trees giving a SR of 0.79, which increased along a gradient of elevation and slope. At the microsite level, female *Taxus* trees were clumped to a scale of 30 m while male trees were randomly distributed. We observed a significant effect of both sex and decade in the growth pattern of *Taxus* trees, where annual radial growth of females was 8.3% greater than that of males. Female trees are more commonly found in wetter sites and males are widely but sparsely distributed, causing the absence of a clear spatial segregation of the sexes. Observed differences in spatial and growth patterns of males and females have the potential to influence the climate change response of *T. baccata* and other dioecious tree species, given that range expansion depends upon the availability of seed-bearing, female trees that tend to be clumped in climatically favorable sites.

Keywords

Dioecy; Tree-ring; Point pattern analysis; Spatial Segregation of the Sexes; Multi-scale approach

Introduction

Ecological differences between males and females in populations of dioecious plants have been demonstrated by several studies (e.g. Bierzychudek and Eckhart 1988). Sex ratio (SR), defined as the proportion of male to female trees, strongly influences the reproductive success and conservation status of dioecious species (Grant and Mitton 1979). Particularly important for reproductive success is the spatial distribution of the sexes that is often influenced by environmental heterogeneity (Hultine et al. 2007). In harsh environments with limited resources, microhabitat differences are responsible for the spatial segregation of the sexes (SSS - Bierzychudek and Eckhart 1988). The underlying hypothesis of SSS is that females require more resources for reproduction than males, leading to the prediction that females are more common in high-resource microsites and males in low-resource microsites (Hultine et al. 2007). The reproductive biology that causes SSS can thus contribute to the vulnerability of dioecious trees to global change because females, requiring a greater reproductive effort, typically show slower growth (de Jong and van der Meijden 2004; Iszkulo et al. 2009). On the poorer sites where males dominate, lower seed availability can contribute to increased potential for regeneration failure in the more resource limited portions of the species range, possibly accelerating species decline on the ―trailing edge‖ in a climate change context (Hampe and Petit 2005). However, if SSS due to niche partitioning is adaptive, then climatic changes could diversify resource availability and a subsequent concentration of females on wetter sites.

The occurrence of male and female plants on different sites, and thus their spatial pattern, can be used as an index of gender-environmental covariance and environmental heterogeneity (Iglesias and Bell 1989). The influences of dioecy on the spatial pattern of tree populations have rarely been studied (Gibson and Menges 1994; Nanami et al. 1999; Hultine et al. 2007), because

47 the majority of studies on dioecious species have been conducted without considering male and
48 female trees separately (e.g. Garcia et al. 2005; Martínez et al. 2010).
49 Spatial point pattern analysis (PPA - Moloney 1993; Wiegand et al. 2007) can be used to analyze
50 spatial association patterns in plant communities (Ripley 1981; Stoyan and Stoyan 1994). These
51 techniques quantify how neighborhood density changes with distance, thus providing a scaling
52 approach that is valuable for describing spatial heterogeneity in community ecology (Levin
53 1992). The contribution of dioecy to the spatial structure of tree communities can be measured by
54 performing a bivariate analysis that shows at different scales if there is significant attraction or
55 repulsion between males and females of the same species.
56 *T. baccata* is a dioecious tree species that plays an important role for the biodiversity of
57 European forests (Linares 2013). *T. baccata* is a relict species that is declining due to poor
58 regeneration (e.g. Sanz et al. 2009), habitat fragmentation (Dubreuil et al. 2010), and reduced
59 genetic variation (e.g. González-Martínez et al. 2010). Other studies have assessed the population
60 structure (Piovesan et al. 2009), structural diversity (Ruprecht et al. 2010), dendrochronological
61 potential (Moir 1999), radial growth (Cedro and Iszkulo 2011), sexual dimorphism (Iszkulo et al.
62 2009) and regeneration pattern (Devaney et al. 2014; Vessella et al. 2015) of *T. baccata*, but
63 sexual variation in distribution pattern and spatial associations among males and females remain
64 unknown. We tested the hypothesis that sex-related trait differences cause spatial segregation of
65 the sexes at three different scales:
66 1. SR varies consistently with water availability as expressed by elevation and precipitation
67 gradients across the species range throughout Europe.
68 2. SR is influenced by water availability as expressed by topographic gradients (elevation
69 slope, continentality) within our 162-ha study area in central Italy.

3. Sex-specific ecological differences cause spatial segregation of the sexes (SSS) at microsite scales: female trees are clustered in more productive sites, whereas males are located on more stressful sites.

Additionally, we hypothesized that resource limitation associated with dioecy influences growth patterns following sexual maturity: male trees grow more than female ones.

Materials and methods

Study area

Macchia delle Tassinete (MdT) has been a floristic protected area since 1974 and is now a Site of Community Importance (SCI) included in the Natura 2000 network (SCI IT5330013). MdT is located in the vicinity of Cingoli village (43°21‘N; 13°12‘E) in the Marche region, central Italy. The research area occupies 162 ha on predominantly north-facing slopes with elevation ranging from 450 to 770 m a.s.l. The bedrock is limestone or marlstone and cambisols of the „Calcic Siltic Chernozem‘ are the dominant soil type. Annual precipitation (1921 - 1990) averages 912 mm and mean annual temperature (1950 - 1990) averages 13°C (Cingoli, 631 m a.s.l.). MdT is classified as a „mesoxeric *Orno-Ostryetum*‘ forest type (IPLA 2001), but tree species dominance changes locally. Most frequent species are *Ostrya carpinifolia* Scop., *Fraxinus ornus* L., *Quercus cerris* L., *Fagus sylvatica* L. and *Taxus baccata* L. Other locally abundant species are *Corylus avellana* L., *Acer opalus* Mill. subsp. *obtusatum* (Waldst. & Kit. ex Willd.) Gams, *Laburnum anagyroides* Medik., *Sorbus torminalis* (L.) Crantz, *Sorbus domestica* L., *Acer platanoides* L., *Quercus pubescens* Willd., and *Acer campestre* L. The current forest structure is the result of previous coppicing on hardwood species and release of *Taxus* standards. The historical presence of *Taxus* at MdT is documented by several historical monuments and documents in the Cingoli

93 village (Avicenna 1644). *Taxus* trees have been protected since 1500, in order to sustainably use
94 their valuable wood and to attract birds for hunting (Appignanesi 1982). However, the entire
95 MdT forest experienced clear-cut harvesting ca. 1870, for land consolidation after the Italian
96 unification process.
97
98 *Field and laboratory methods*
99 In 2011, all *Taxus* trees having a DBH > 15 cm were tagged and mapped with a Trimble GeoXT
100 GPS receiver and a differential correction through Pathfinder Office 4.2 software was performed
101 (0.5-1 m estimated accuracy). For each of 1030 mapped *Taxus* trees, we recorded sex, DBH, total
102 height, canopy height, and four canopy radii. Sex could be determined for 951 (92.3%) of *Taxus*
103 trees.
104 From a subsample of 10% of *Taxus* trees, selected according their diameter frequency
105 distribution, we collected two orthogonal wooden cores per tree (189 cores, 110 trees) at 1.3 m
106 height to perform a standard dendrochronological analysis. In the laboratory, all cores were glued
107 to grooved wooden mounts and sanded to a high polish until optimal surface resolution allowed
108 annual rings to be detected under magnification.
109
110 *Data analyses*
111 We assessed the spatial heterogeneity of tree sex distribution adopting a multi-scale approach.
112 At the species range scale (Europe), we compared the SR of our study site with SR of other *T.*
113 *baccata* forests by using literature data (Dhar et al. 2008; Iszkulo et al. 2009; Vessella et al.
114 2015), and used simple linear regression analysis to quantify relationships between SR and
115 elevation, and SR and annual precipitation. At the landscape scale, we explored SR behavior

116 within our study site through regression analysis along tree structural (DBH and height) and
117 environmental (elevation, slope and distance from the Adriatic Sea) gradients.
118 At the microsite scale, univariate and bivariate Point Pattern Analyses (PPA) were applied
119 to a data set of mapped *Taxus* locations (Moeur 1993) to assess tree spatial patterns within the
120 study area and the spatial associations between the two sexes or two DBH classes across spatial
121 scales from 0 – 50 m. The spatially explicit dataset that was used in the analyses comprised 419
122 males and 532 females, 784 small (DBH < 30 cm) and 56 large (DBH > 40 cm) trees. We used
123 pair-correlation functions *g* (r) (Stoyan and Stoyan 1994) to avoid possible misinterpretation of
124 results due to the cumulative effect typically found in other methods such as *K*-function analysis
125 (Ripley 1977; Perry et al. 2006). The univariate pattern of *Taxus* trees as a whole was contrasted
126 against the heterogeneous Poisson null model to account for first-order effects. This null model
127 differs from complete spatial randomness (CSR) in that a function $\lambda(x, y)$ varies with location (x,
128 y) but maintains the independence of the occurrence of any point with respect to any other
129 (Wiegand and Moloney 2004). For the bivariate analyses between males vs. females and small
130 vs. large trees, we applied the random labeling null model that simply randomizes tree category
131 without changing geographic position (Wiegand and Moloney 2004). The latter is a conservative
132 method to test the significance of spatial association between two categories (e.g. males vs
133 females). The 95% confidence intervals for both univariate and bivariate analyses were computed
134 from 999 Monte Carlo simulations (Stoyan and Stoyan 1994; Wiegand and Moloney 2004) and
135 the goodness-of-fit (GoF) test for null hypothesis was performed (Diggle 2003). All analyses
136 were done only for classes with more than 15 trees (Camarero et al. 2000), applying a 1 m lag
137 distance and a maximum distance of 100 m with the grid-based software Programita (Wiegand
138 and Moloney 2004) adopting a grid size of 1 m2 and a ring width of 5 m.

Tree-ring widths were measured using a LINTAB semi-automatic optical system (Rinntech 2003) at a precision of 0.001 mm. All tree-ring series were first visually and then statistically checked for cross-dating and measurement errors using the CDI (Cross Dating Index) run by TSAP-Win software (Rinntech 2003). Mean tree-ring chronologies for male and female *Taxus* trees were compiled from selected crossdated series using the ARSTAN program (Cook and Holmes 1997). To remove interannual frequency variations each tree-ring series was standardized with a spline function using a 50% frequency response. Statistical indices were calculated on a common interval of 100 years (1909-2009) in order to compare male and female chronologies. Tree-ring statistics included: the mean sensitivity (MS) which is the mean percent change from each measured yearly ring value to the next to assess the high-frequency variation of the series (Fritts 1976); the first-order autocorrelation on raw (AC) and standardized data (AC1); the average correlation between series (RBAR) that was calculated for all series using the running means method on overlay periods of 50 and 25 years; the Expressed Population Signal (EPS), a measure of how the mean chronology derived from the sample trees represents a hypothetical infinite replicated chronology (Wigley et al. 1984). Additionally, cumulative ring width and basal area increment (BAI) curves were obtained from the mean chronologies of male and female trees.

A general linear mixed-effects model (GLMM) was used to detect radial growth differences between males (n = 32) and females (n = 38) over the 1920 – 2010 time period. Radial growth (decadal mean) was log transformed prior to analysis, to normalize distributions and stabilize variance of residual errors. Log transformed radial growth (RG-ln) was used as the response variable and sex and decade were used as independent factors. Individual tree identity was specified as a random intercept term to allow the overall growth rate to vary by tree (accounting for differences in genetics, microsite variability, etc.). GLMM was fitted by using the Linear and

Nonlinear Mixed Effects Models package (nlme 3.1-105 ver.) within the R statistical software (2.15.2 ver.).

Results

Sex ratio at broad scales

We found 419 males and 532 females, giving an overall SR of 0.79 (Table 1). Males were slightly larger (25.6 cm VS 25.14 cm DBH) and shorter (6.52 m VS 6.65 m height) than females, but these differences were not significant (t = 0.729; p = 0.47 for DBH and t = -1.02; p = 0.309 for height).

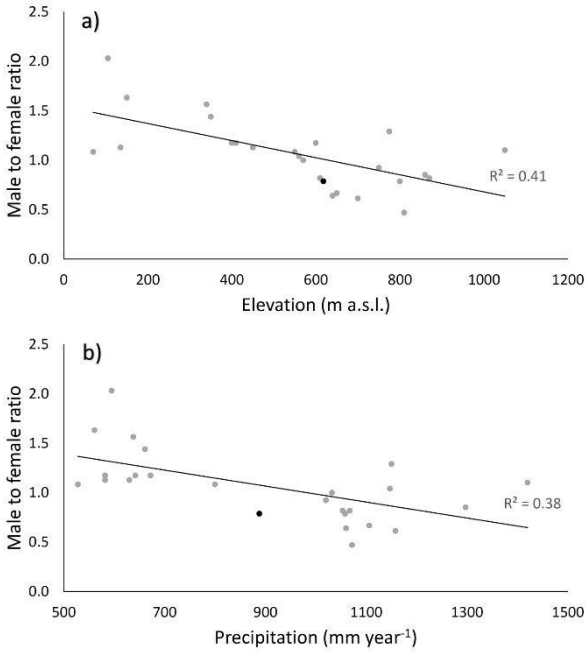
Table 1. Summary statistics (mean, median and standard error) of structural attributes and environmental variables of *Taxus* trees at MdT study site. DBH = diameter at breast height (cm); H = height (m), V = Volume (m3).

SEX (n)	Statistics	DBH (cm)	H (m)	Crown H (m)	Crown V (m^3)	Elevation (m a.s.l.)	Slope (°)	Sea Dist. (Km)
Males (419)	Mean	25.61	6.52	1.89	77.35	700.76	24.23	39.73
	Median	24.00	6.50	1.90	58.11	700.00	25.20	39.79
	SE	0.47	0.09	0.03	3.42	1.11	0.33	0.02
Females (532)	Mean	25.14	6.65	1.98	80.31	699.05	22.72	39.78
	Median	23.00	6.50	2.00	56.37	699.22	23.62	39.85
	SE	0.41	0.08	0.02	3.91	0.87	0.31	0.01
Undetermined (79)	Mean	25.01	6.95	1.80	99.92	640.66	21.63	39.33
	Median	22.00	6.60	1.80	62.30	681.12	24.69	39.33
	SE	1.08	0.24	0.07	10.47	8.68	1.21	0.07

174 At the species range scale, the MdT study site occupies an intermediate position in a topo-
175 climatic gradient of 24 European research studies reporting the SR of *Taxus* (Fig. 1). The MdT
176 site fits within an annual precipitation range (750 – 950 mm) that was rarely considered in
177 previous studies, and has a lower SR than expected for its precipitation level. Across the range of
178 *T. baccata*, the SR decreased with increasing elevation and precipitation.

179

180 **Figure 1**. Male to female ratio (SR) observed at MdT (black dot) related to elevation (a) and precipitation (b)
181 compared to other 25 European forests (grey dots) with *T. baccata* (Dhar et al. 2008; Iszkulo et al. 2009; Vessella et
182 al. 2015).



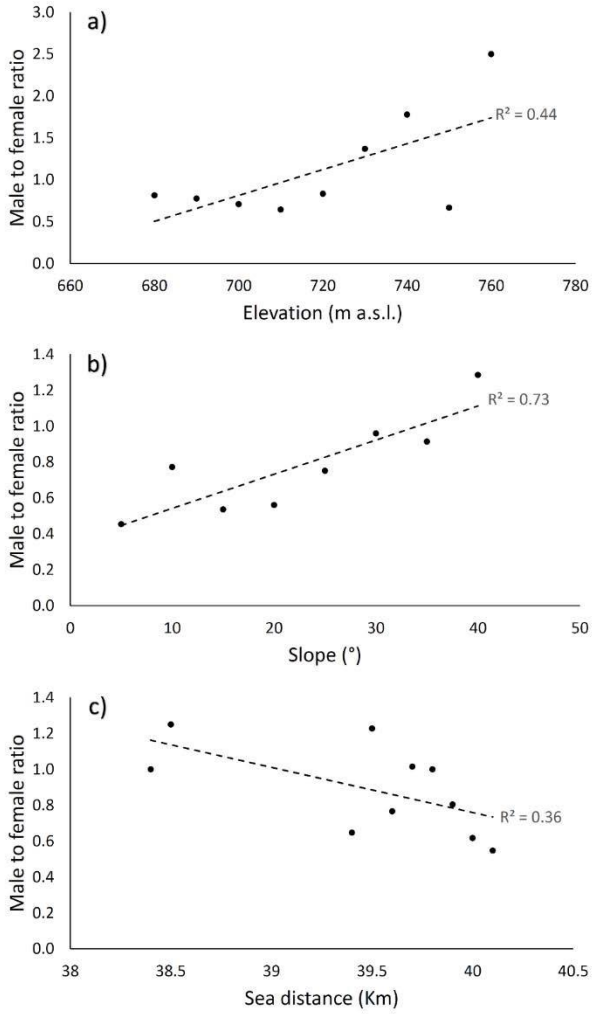
183

184

185 At the landscape scale, SR increased with elevation and slope steepness and decreased with
186 distance to the Adriatic Sea (Fig. 2). SR approximated unity in those sites located at lower
187 elevations and closer to the sea.

188

Figure 2. Male to female ratio (SR) observed at MdT against environmental gradients of elevation (a), slope (b) and distance from the Adriatic Sea (c).

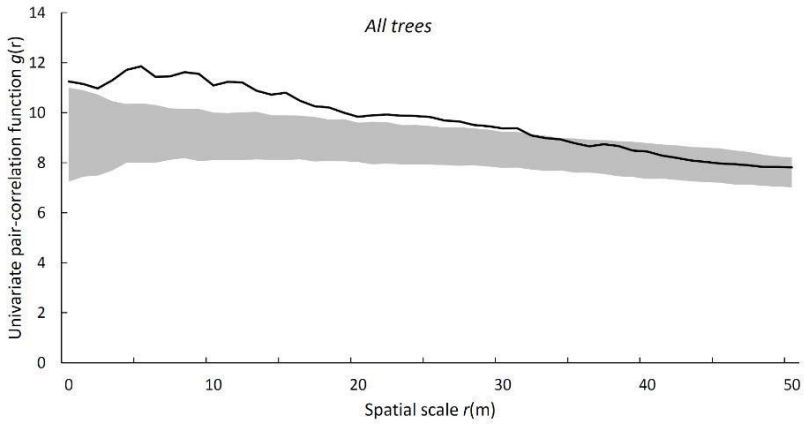


Fine scale spatial pattern

Taxus trees, pooled among both sexes and all DBH classes, showed significant aggregation ($p \leq 0.01$) to a distance of 30 m (Fig. 3).When considered separately in univariate analyses (Fig. 4), males were randomly distributed, while females were weakly grouped ($p \leq 0.01$) at 15 and 35-40 m. The univariate g (r) function showed a clear tendency towards aggregation ($p \leq 0.01$) for small trees, whereas large trees were randomly distributed. By assessing the univariate pattern of a

combination between DBH and sex, we observed a similar pattern in males and females. Small trees were weakly aggregated ($p \leq 0.01$) while large trees were randomly distributed.

Figure 3. Univariate analysis of the spatial pattern of 1030 *Taxus* trees at MdT. The bold line indicates the pair-correlation function g(r), and shaded areas encompass the non-significant, i.e. random, distribution and represent points within the 2.5th and 97.5th percentile g(r) values of the 999 simulations of the null model assuming a heterogeneous Poisson distribution.



The bivariate spatial association between sexes showed a random pattern (Fig. 5). However, significant spatial segregation ($p \leq 0.01$) was observed between small and large diameter trees, with stronger segregation for males than for females.

Figure 4. Univariate analysis ofthe spatial pattern of *Taxus* trees, considering sex (males and females), DBH (small and large), and their combinations (e.g. small males and large females), using the pair-correlation function g(r). Black lines indicate the pair-correlation functions g(r), and shaded areas encompass random distribution and represent points within the 2.5th and 97.5th percentile g(r) values ofthe 999 simulations ofthe null model (Random Labeling).

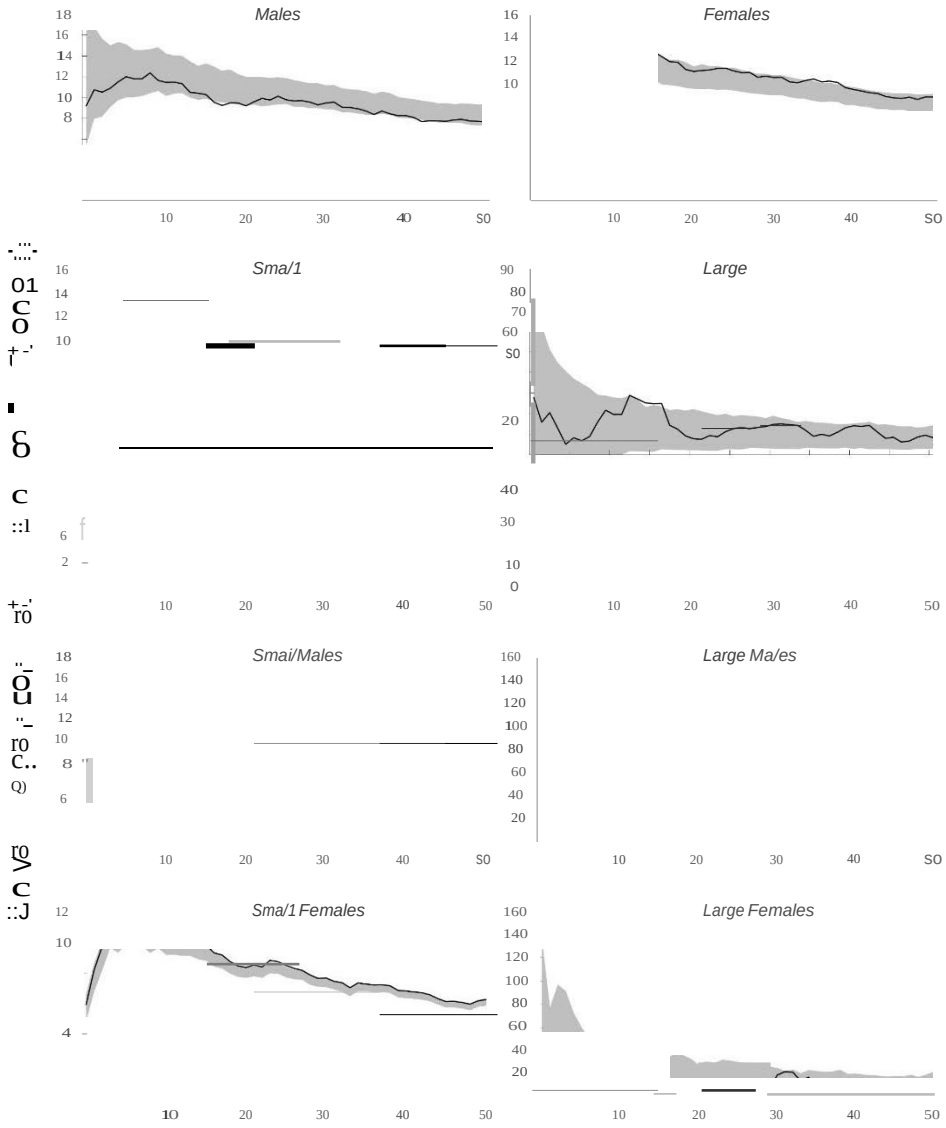
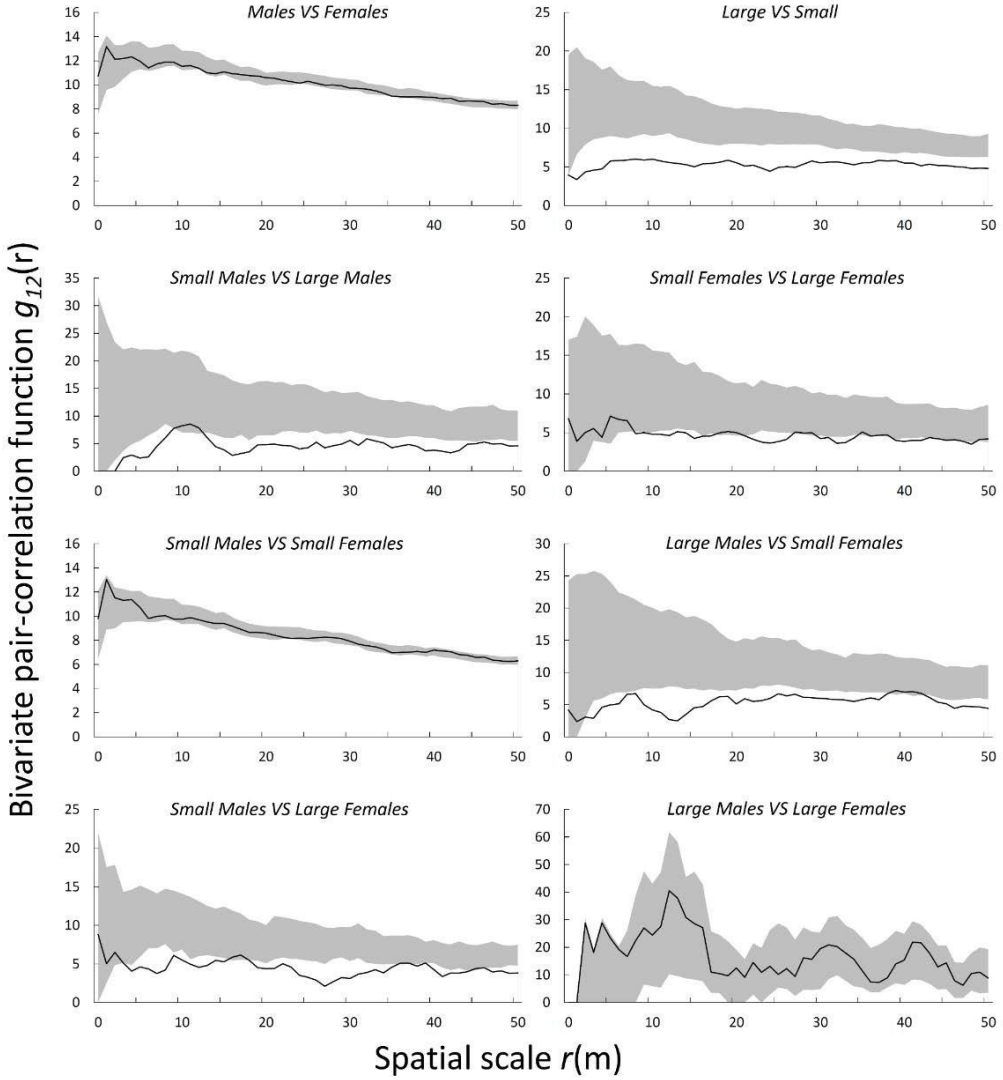


Figure 5. Bivariate analysis of the spatial pattern of *Taxus* trees, considering sex (males and females) and DBH (small and large), and their combinations (e.g. small males VS large females), using the pair-correlation function g12(r). Black lines indicate the pair-correlation functions g12(r), and shaded areas encompass random distribution and represent points within the 2.5th and 97.5th percentile g12(r) values of the 999 simulations of the null model (Random Labeling).



Growth pattern

Male and female tree-ring chronologies were well crossdated and showed similar values in most dendrochronological descriptors (Table 2): time spans were 1879-2010 for males and 1881-2010

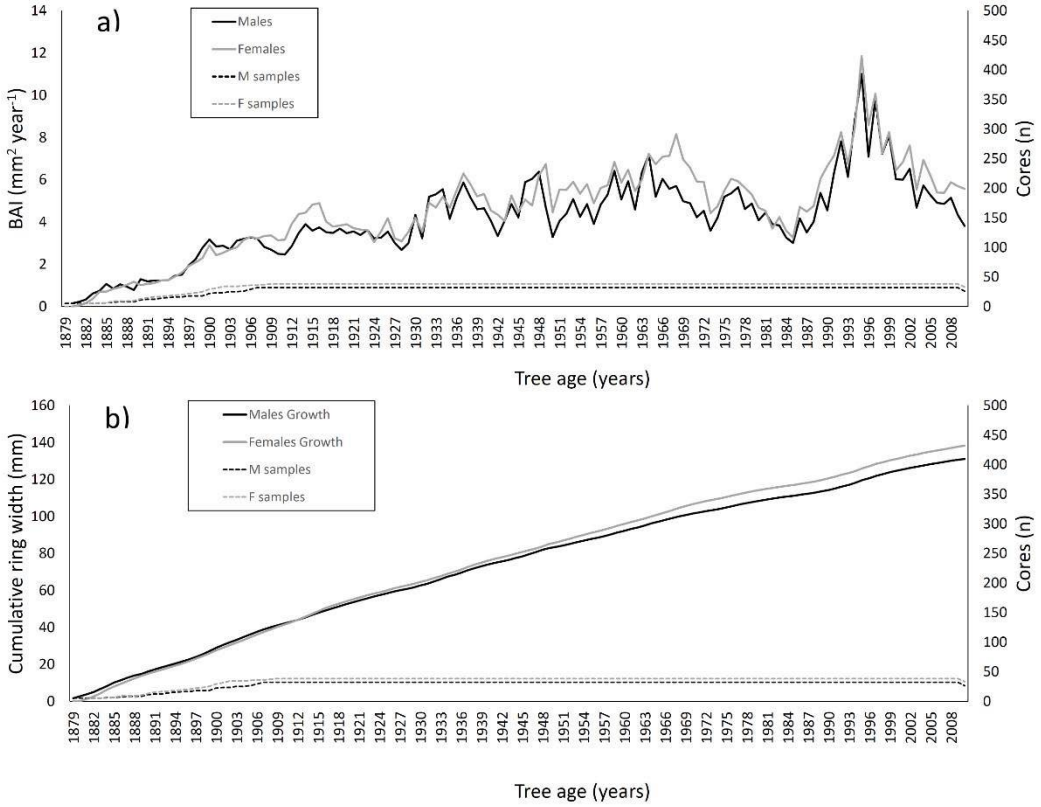
for females. Males and females showed similar mean ring width (0.99 mm and 1.06 mm), mean sensitivity (high-frequency variability), first-order autocorrelation (low-frequency variability), correlation between tree-ring series (Rbar), and adequacy of the chronologies (EPS). The two BAI curves (Fig. 6a) show similar trends particularly in recent years, with a growth oscillation of approximately 30 yrs caused by a coppice rotation cut on hardwood species in 1984 and the resulting canopy regrowth. The periods of greatest differences between male and female growth were 1907-1915, 1943-1959, and 1963-1975. Finally the cumulative ring width curves showed a coincident growth pattern of male and female *Taxus* trees up to the 1950‘s and a slightly increasing divergence thereafter (Fig. 6b).

The GLMM showed a significant effect of sex on radial growth of *Taxus* trees (p = 0.028). Annual radial growth of female trees was 8.3% greater than that of male trees (95% CI: 0.9% to 15.1%), after accounting for decade of growth and the random effects of growth variability among individuals growing in different microsites.

Table 2. Comparison of males and females chronologies by common statistical dendrochronology indices (MRW: mean ring width; MI = mean index value; Rbar = average correlation between series; EPS = expressed population signal; MS = mean sensitivity of the average chronology; AC1 = first-order autocorrelation on raw data; AC = autocorrelation on standardized data).

Series (n)	Time Interval (yrs)	Common Interval (yrs)	MRW (mm)	MI	Rbar	EPS	MS	AC1	AC
Males (32)	1879-2010	1909-2009	0.99	0.97	0.16	0.86	0.16	0.7	-0.1
Females (38)	1881-2010	1909-2009	1.06	0.98	0.14	0.86	0.12	0.8	-0.2

Figure 6. Basal Area Increment (a) and cumulative ring width for males (n = 32) and females (n = 38) at MdT study site. Continuous lines indicate BAI and cumulative ring width and dotted lines indicate the number of sampled cores.



Discussion

Sex ratio at species range and landscape scales

At the regional scale, our study site occupies an intermediate position along a European environmental gradient where the SR decreased with increasing elevation and precipitation (Fig. 2). We observed SRs that were female-biased, and lower than would be expected given regional levels of precipitation and elevation. Female-biased populations have also been found on wetter sites in the Alps (Hilfiker et al. 2004) and in the Andes (Nuñez et al. 2008), adding support to the hypothesis that the proportion of females increases with water availability.

At the landscape-scale in our MdT study area, we observed a high SR on steeper, higher elevation sites, the opposite relationship as observed for the regional-scale comparisons. This apparent discrepancy likely arises because the sites closer to the ridge are more water-limited because of shallow, rocky soils, and thus are least favorable for female *Taxus* trees. On the contrary, at a regional scale higher elevation sites coincided with increased water availability (Iszkulo et al. 2009).

Males were less abundant than females at MdT and the difference between them in tree size (DBH and height) was not significant. These findings are partly discordant with other studies on *T. baccata* of central Europe that found larger and more abundant males on drier sites (Iszkulo et al. 2009).

SR increased with increasing diameter, but decreased with increasing height consistently with other European studies on SR of *Taxus* trees (e.g. Iszkulo et al. 2009). Taken together, these data suggest that males put more carbon into diameter growth, and females into height growth, when they are in the older growth stages. However, this could also be a matter of where they grow: possibly the females, growing on the wetter sites, have more side-pressure from competing trees and so allocate more carbon to height growth.

Influence of dioecy on spatial patterns at microsite scales

Adult *Taxus* trees (DBH > 15 cm) were strongly grouped at fine spatial scales (< 30 m) at MdT, probably representing a pattern of repeated clustering. On the contrary, other authors have found random distribution in adult *Taxus* trees (Martinez et al. 2010). Considering the two sexes separately, we observed a weak but clustered pattern in females and a random pattern in males. The observed patterns were consistent with the hypothesis of males being the more stress tolerant

293 that can occupy a broader spectrum of suitable microsites (Hultine et al. 2007; Iszkulo et al.
294 2009).

295 We did not find spatial segregation of the sexes (SSS) at MdT, meaning that there was not
296 significant aggregation nor repulsion between males and females. This was probably because
297 female trees were clustered and more common in wetter portions of the elevation gradient,
298 whereas males were widely distributed. Homogeneity of habitats at fine scales can be another
299 possible cause of absence of spatial segregation of the sexes (Ueno et al. 2007; Schmidt 2008;
300 Iszkuło et al. 2011). However, female *Taxus* trees at MdT exhibited a clear tendency towards
301 clustering in wetter sites. Another possible explanation for the absence of SSS at MdT could be
302 that seed dispersal in *T. baccata* is primarily by birds causing a wide distribution of seeds
303 (Hubbell 1979; Murray 1988) that can in turn weaken the effect of dioecy on the spatial
304 heterogeneity of trees (Nanami et al. 1999). Birds can spread seeds across long distances, but
305 often distribute seeds in a clustered manner (e.g. burial sites for seed-caching species; below
306 favorite roosting sites).

307 Nevertheless, we found spatial segregation between smaller and larger trees, a pattern
308 already described for adult *Taxus* trees and regeneration in other European sites (Dovčiak 2002;
309 Piovesan et al. 2009; Devaney et al. 2014). As expected, small trees were aggregated for both
310 males and females, whereas large trees were randomly distributed. The spatial segregation
311 between smaller and larger trees is probably due to a negative intraspecific neighborhood effect
312 that has been previously reported for *T. baccata* (Dovčiak 2002; Piovesan et al. 2009; Devaney et
313 al. 2014) and for other species (He and Duncan 2000). Moreover, the traditional coppice system
314 with dense *Taxus* standards may have favored the establishment of *Taxus* regeneration into forest
315 canopy gaps close to adult *Taxus* trees.

316

317 *Influence of dioecy on growth patterns*

318 The mean chronologies of male and female *Taxus* trees emerged as being very similar showing
319 that the overall growth patterns were analogous. However, despite wide variability among
320 individual trees, female *Taxus* trees in our study area showed a significantly higher growth rate.
321 Nonetheless, other authors have reported a radial growth reduction of female trees associated
322 with the achievement of sexual maturity in the studied population (e.g. Obeso 2002; Bañuelos
323 and Obeso 2004; Cedro and Iszkulo 2011). Female individuals may require more resources than
324 males because of higher reproduction effort (Iszkulo et al. 2009). A possible explanation of the
325 counter-intuitive pattern observed at MdT is that female growth can be favored by the more
326 productive sites that they occupy, as opposed to males that occur across a wide variety of
327 microsite conditions. Where female trees of dioecious species occupy more favorable sites than
328 males, greater resource availability may compensate for greater reproductive requirements. Other
329 authors found no significant differences between sexes in *Araucaria angustifolia* mean radial
330 growth in South America, but they observed a higher growth rate of females in the last two
331 decades (Cattaneo et al. 2013).

332 Our results highlight that in order to relate observed spatial patterns in dioecious species
333 to habitat conditions, we need to consider abiotic and biotic constraints of tree establishment.
334 Future research should investigate the spatial pattern of male and female trees along wide
335 environmental gradients, in order to better understand the role of climate and topography in the
336 SSS process. Site conditions, habitat variability, and water availability in particular are expected
337 to strongly influence the strength of segregation between sexes in dioecious species (Dawson and
338 Bliss 1989; Dudley 2006). Spatial distribution modeling of dioecious species requires accounting
339 for the different resource requirements and distribution patterns of male and female trees,

particularly in the climate change context where range expansion to favorable sites depends upon the availability of seed-bearing, female trees (Tognetti et al. 2012; Hultine et al. 2013).

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References

Appignanesi P (1982) Il tasso nella storia e nella cultura di Cingoli. In: Pedrotti F (eds) Guide – Itinéraire de l'excursion internationale de phytosociologie en Italie Centrale (2-11 juillet 1982). International Society for Vegetation Science, Camerino, pp 182-187

Avicenna O (1644) Memorie della Città di Cingoli. Ercolani, Jesi

Bañuelos MJ, Obeso JR (2005) How is fruit production regulated in the dioecious fleshy-fruited shrub Rhamnus alpinus? Basic Appl Ecol 6(3): 249-259

Bierzychudek P, Eckhart V (1988) Spatial segregation of the sexes of dioecious plants. Am Nat 132(1): 34-43

Camarero JJ, Gutiérrez E, Fortin MJ (2000) Spatial pattern of subalpine forest-alpine grassland ecotones in the Spanish Central Pyrenees. Forest Ecol Manag 134(1): 1-16

362 Cattaneo N, Pahr N, Fassola H, Leporati J, Bogino S (2013) Sex-related, growth-climate
363 association of Araucaria angustifolia in the neotropical ombrophilous woodlands of
364 Argentina. Dendrochronologia 31: 147-152
365 Cedro A, Iszkulo G (2011) Do females differ from males of European yew (*Taxus baccata* L.) in
366 dendrochronological analysis? Tree-Ring Res 67(1): 3-11
367 Cook ER, Holmes RL (1986) Users manual for program ARSTAN. Laboratory of Tree-Ring
368 Research, University of Arizona, Tucson
369 Dawson TE, Bliss LC (1989) Patterns of water use and the tissue-water relations in the dioecious
370 shrub, Salix arctica. The physiological basis for habitat partitioning between the sexes.
371 Oecologia 79: 332–343
372 de Jong TJ, van der Meijden E (2004) Sex ratio of some long-lived dioecious plants in a sand
373 dune area. Plant Biol 6(5): 616-620
374 Devaney JL, Jansen MA, Whelan PM (2014) Spatial patterns of natural regeneration in stands of
375 English yew (*Taxus baccata* L.); Negative neighbourhood effects. Forest Ecol Manag 321:
376 52-60
377 Diggle PJ (2003) Statistical analysis of spatial point patterns. Oxford University Press, New York
378 Dhar A, Ruprecht H, Vacik H (2008) Population viability risk management (PVRM) for in situ
379 management of endangered tree species—A case study on a *Taxus baccata* L. population.
380 Forest Ecol Manag 255: 2835-2845
381 Dovčiak M (2002) Population dynamics of the endangered English yew (*Taxus baccata* L.) and
382 its management implications for biosphere reserves of the Western Carpathians. Mab
383 UNESCO, Paris
384 Dubreuil M, Riba M, González-Martínez SC, Vendramin GG, Sebastiani F, Mayol M (2010)
385 Genetic effects of chronic habitat fragmentation revisited: strong genetic structure in a

386 temperate tree, *Taxus baccata* (Taxaceae), with great dispersal capability. Am J Bot 97(2):
387 303-310
388 Dudley L (2006) Ecological correlates of secondary sexual dimorphism in Salix glauca
389 (Salicaceae). Am J Bot 93: 1775–1783
390 Fritts HC (1976) Tree rings and climate. Academic, San Diego
391 Garcia D, Obeso JR, Martinez I (2005) Spatial concordance between seed rain and seedling
392 establishment in bird-dispersed trees: does scale matter? J Ecol 93(4): 693-704
393 Gibson DJ, Menges ES (1994) Population structure and spatial pattern in the dioecious shrub
394 Ceratiola ericoides. J Veg Sci 5(3): 337-346
395 González-Martínez SC, Dubreuil M, Riba M, Vendramin GG, Sebastiani F, Mayol M (2010)
396 Spatial genetic structure of *Taxus baccata* L. in the western Mediterranean Basin: Past and
397 present limits to gene movement over a broad geographic scale. Mol Phylogenet Evol 55(3):
398 805-815
399 Grant MC, Mitton JB (1979) Elevational gradients in adult sex ratios and sexual differentiation in
400 vegetative growth rates of *Populus tremuloides* Michx. Evolution 33(3): 914-918
401 Hampe A, Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters.
402 Ecol Lett 8: 461-467
403 Hilfiker K, Holderegger R, Rotach P, Gugerli F (2004) Dynamics of genetic variation in *Taxus*
404 *baccata*: local versus regional perspectives. Can J Bot 82(2): 219-227
405 He F, Duncan RP (2000) Density-dependent effects on tree survival in an old-growth Douglas fir
406 forest. J Ecol 88(4): 676-688
407 Hubbell SP (1979) Tree dispersion, abundance, and diversity in a tropical dry forest. Science
408 203(4387): 1299-1309

409 Hultine KR, Bush SE, West AG, Ehleringer JR (2007) Population structure, physiology and
410 ecohydrological impacts of dioecious riparian tree species of western North America.
411 Oecologia 154(1): 85-93
412 Hultine KR, Burtch KG, Ehleringer JR (2013) Gender specific patterns of carbon uptake and
413 water use in a dominant riparian tree species exposed to a warming climate. Global Change
414 Biol 19: 3390-3405
415 Iglesias MC, Bell G (1989) The small-scale spatial distribution of male and female plants.
416 Oecologia 80(2): 229-235
417 IPLA, Regione Marche (2001) I tipi forestali delle Marche. Diffusioni Grafiche, Torino
418 Iszkuło G, Jasińska AK, Giertych MJ, Boratyński A (2009) Do secondary sexual dimorphism and
419 female intolerance to drought influence the sex ratio and extinction risk of *Taxus baccata*?
420 Plant Ecol 200(2): 229-240
421 Iszkuło G, Jasińska AK, Romo A, Tomaszewski D, Szmyt J (2011) The greater growth rate of
422 male over female of the dioecious tree Juniperus thurifera only in worse habitat conditions.
423 Dendrobiology 66: 15–24
424 Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73: 1943-1967
425 Linares JC (2013) Shifting limiting factors for population dynamics and conservation status of
426 the endangered English yew (*Taxus baccata* L., Taxaceae). Forest Ecol Manag 291: 119-127
427 Martínez I, Wiegand T, González-Taboada F, Obeso JR (2010) Spatial associations among tree
428 species in a temperate forest community in North-western Spain. Forest Ecol Manag 260(4):
429 456-465
430 Moeur M (1993) Characterizing spatial patterns of trees using stem-mapped data. Forest Sci
431 39(4): 756-775

Moloney KA (1993) Determining process through pattern: reality or fantasy? In: Levin SA, Powel TM, Steele JW (eds) Patch Dynamics. Springer-Verlag, Heidelberg, pp 61-69

Moir AK (1999) The dendrochronological potential of modern yew (*Taxus baccata*) with special reference to yew from Hampton Court Palace, UK. New Phytol 144(3): 479-488

Murray KG (1988) Avian seed dispersal of three neotropical gap-dependent plants. Ecol Monogr 58(4): 271-298

Nanami S, Kawaguchi H, Yamakura T (1999) Dioecy-induced spatial patterns of two codominant tree species, *Podocarpus nagi* and *Neolitsea aciculata*. J Ecol 87(4): 678-687

Nuñez CI, Nuñez MA, Kitzberger T (2008) Sex-related spatial segregation and growth in a dioecious conifer along environmental gradients in northwestern Patagonia. Ecoscience 15(1): 73-80

Obeso JR (2002) The costs of reproduction in plants. New Phytol 155(3): 321-348

Perry GL, Miller BP, Enright NJ (2006) A comparison of methods for the statistical analysis of spatial point patterns in plant ecology. Plant Ecol 187(1): 59-82

Piovesan G, Saba EP, Biondi F, Alessandrini A, Di Filippo A, Schirone B (2009) Population ecology of yew (*Taxus baccata* L.) in the Central Apennines: spatial patterns and their relevance for conservation strategies. Plant Ecol 205(1): 23-46

Rinntech (2003) TSAP-Win. Time Series Analysis and Presentation for Dendrochronology and Related Applications. User Reference. Rinntech, Heidelberg

Ripley BD (1981) Spatial statistics. Hayward Wiley, New York

Ripley BD (1977) Modelling spatial patterns. J Roy Stat Soc B Met 39(2): 172-212

Ruprecht H, Dhar A, Aigner B, Oitzinger G, Klumpp R, Vacik H (2010) Structural diversity of English yew (*Taxus baccata* L.) populations. Eur J For Res 129(2): 189-198

455 Sanz R, Pulido F, Nogués-Bravo D (2009) Predicting mechanisms across scales: amplified
456 effects of abiotic constraints on the recruitment of yew *Taxus baccata*. Ecography 32(6):
457 993-1000
458 Schmidt JP (2008) Sex ratio and spatial pattern of males and females in the dioecious sandhill
459 shrub, *Ceratiola ericoides ericoides* (Empetraceae) Michx. Plant Ecol 196: 281–288
460 Stoyan D, Stoyan H (1994) Fractals, random shapes, and point fields: methods of geometrical
461 statistics. Wiley, Chichester
462 Tognetti R (2012) Adaptation to climate change of dioecious plants: does gender balance matter?
463 Tree Physiol 32: 1321-1324
464 Ueno N, Suyama Y, Seiwa K (2007) What makes the sex ratio female-biased in the dioecious
465 tree *Salix sachalinensis*? J Ecol 95: 951–959
466 Vessella F, Salis A, Scirè M, Piovesan G, Schirone B (2015) Natural regeneration and gender-
467 specific spatial pattern of *Taxus baccata* in an old-growth population in Foresta Umbra
468 (Italy). Dendrobiology 73: 75-90
469 Wiegand T, Moloney AK (2004) Rings, circles, and null-models for point pattern analysis in
470 ecology. Oikos 104(2): 209-229
471 Wiegand T, Gunatilleke S, Gunatilleke N (2007) Species associations in a heterogeneous Sri
472 Lankan dipterocarp forest. Am Nat 170(4): E77-E95
473 Wigley TM, Briffa KR, Jones PD (1984) On the average value of correlated time series, with
474 applications in dendroclimatology and hydrometeorology. J Clim Appl Meteorol 23(2): 201-
475 213